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Effect of Nursery Short Day and Drought Treatments on Development and Early Farm-field Performance of Western Redcedar

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SUMMARY

The study describes first-year growth of containerized western redcedar seedlings, including growth rates for several morphological characters, apical transitions in leaf initiation, and stomatal distribution on leaf and cotyledon surfaces.

One-year-old container grown seedlings of western redcedar (*Thuja plicata* Donn.) were subjected to short (8-h) day stress (SD) and/or moisture stress (DR) and their response compared to that of untreated seedlings. The treatments were applied at various times during the growing season and lasted 2 and 4 weeks. Seedling height was the only morphological character that could be effectively controlled by the above cultural regimes: SD slowed shoot growth only when applied during the most rapid period of shoot elongation in late June and early July; SD combined with DR always reduced the final height regardless of the time and duration of applied treatments. None of the treatments substantially affected root collar diameter and root dry weight, but the 2-week treatments yielded seedlings with larger root collar diameter and root dry weight than did 4-week treatments. Moderate DR applied alone in mid-August hastened root dry weight gain, but did not affect other morphological characters.

The applied treatments had no lasting effects on mitotic activity of terminal shoot apices and resulted in no differences in the timing of fall growth cessation. Dormancy release results indicate there is some endogenous control during overwintering of seedlings of this species which would not be detected under prolonged photoperiod conditions. Possibly some chilling requirement must be satisfied for the leader to resume growth but not necessarily for the lateral shoots. Acquisition of frost hardiness was delayed by DR treatments.

The tallest nursery stock was still the tallest after the first field-growing season. Stock planted in wet beds had greater height increment than that planted in dry beds. Nursery treatments did not effect stock storability.

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1 INTRODUCTION

Western redcedar (*Thuja plicata* Donn.) is a member of the Cupressaceae family. In contrast to the Pinaceae, the Cupressaceae have a distinctly different type of shoot growth (Zobel 1983). They do not possess overwintering buds covered by bud scales or a preformed shoot (Pillai 1963; Owens and Molder 1974; Harry 1987; Parker and Johnson 1987). Rather, the apical meristem is covered by leaf primordia at various stages of development.

Studies of shoot growth, particularly branching patterns, have been presented for some species of the Cupressaceae, including western redcedar (Parker and Johnson 1987). However, first-year growth of western redcedar seedlings and environmental factors influencing seedling morphology and physiology have not been studied in detail. Changes in day length and moisture regimes are now being used to control seedling development in container nurseries for many of the Pinaceae (Lavender and Cleary 1974), but no studies have yet been made on how similar changes affect seedling growth in the Cupressaceae. This study evaluated the utility of changes in day length and moisture regimes in controlling first-year growth and development of western redcedar seedlings in styroblock containers under production nursery conditions.

2 MATERIALS AND METHODS

2.1 Seed Source and Nursery Culture

Seedlot 4511 (from the Port McNeill area, B.C., elevation 600 m) was grown in PSB 313A styroblocks at the MacMillan Bloedel, Angus P. MacBean nursery in Cedar, B.C. (49° 5" N, elevation 97 m). Seeds were sown on March 20, 1987, and March 10, 1988. Styroblock cavities were filled with a 1:2 mixture of vermiculite and peat moss, nutricote 16-10-10 (type 270, 3.4 kg/m^3, and type 360, 4.6 kg/m^3 in 1987 and 1988, respectively), 1.5 kg/m^3 of dolomite lime (Green Valley), and 300 g/m^3 of Micromax trace elements.

Styroblocks were misted daily with water during germination and subsequently when block weight fell 2.5 kg below saturated weight. Xylem tension measurements were made periodically at about 09.00. Seedlings were watered when the xylem tension was between -0.65 and -0.85 MPa; the xylem tension of drought-stressed seedlings was allowed to reach -0.95 to -1.1 MPa (E. A. Maher, Manager, A.P. MacBean Nursery, pers. comm.). Daily temperatures and relative humidity were recorded with an "Argus" computerized monitoring system. The data for the experimental period are shown in Figures 1–2.

Seedlings were fertilized with N-P-K every 4-7 days during the growing season and chelated trace elements were added at 10 g/kL with all applications in both years.

2.2 The Nursery Treatments and Experimental Design

In 1987, the seedlings were subjected to short day (SD), 8-h photoperiods combined with a moisture stress (DR), or no moisture stress (ND) at three starting dates (July 7 and 21, August 4) for 2 and 4 weeks. Another treatment was started on August 18 (Aug. DR), consisting of a 2-week DR and ambient day length (AD). Controls were grown at AD and ND throughout the growing season. This resulted in 14 treatment combinations including the control (Table 1). In 1988, SD, DR, and SD X DR were applied for 2 weeks at two starting dates (June 30, July 15) (Table 1).

In 1987, the experiment was a split plot design with no replicates and styroblocks were organized in a greenhouse in rows by treatments. A split plot with no replicates was also used in 1988 but styroblock location was completely randomized. A buffering zone was created around the experimental styroblocks to eliminate edge effects.

The field experiment was designed with beds as the whole plot and the six nursery treatments (except treatment No. 4, Table 1), with three 15-tree replications on two planting dates, as the split plot.

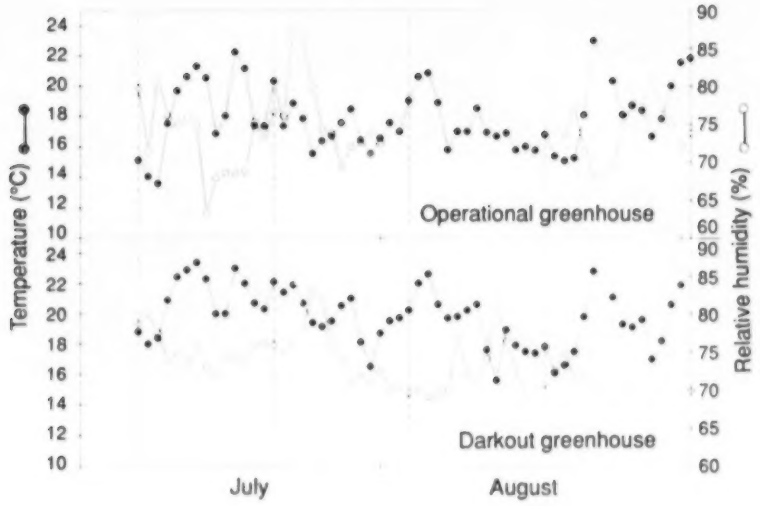


FIGURE 1. Temperature and relative humidity versus time in 1987. Dashed vertical lines indicate treatment starting dates (July 7, 21; August 4, 18). Note: Because of computer failure the data on relative humidity in the operational greenhouse were not available in early to mid-August.

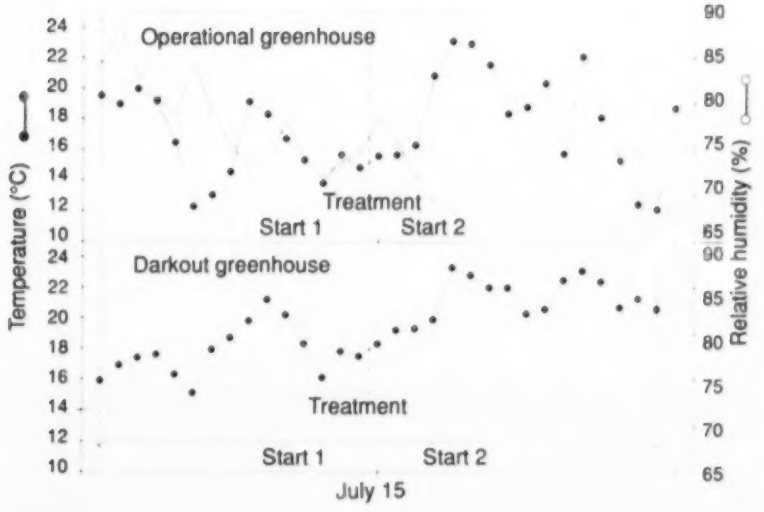


FIGURE 2. Temperature and relative humidity versus time in 1988. Dashed vertical lines separate the 2-week periods of treatment applications (June 30–July 14, July 15–30).

TABLE 1. Treatment types, durations, and dates of treatment application in the 1987 and 1988 experiments

Growing season	#	Applied treatments		
		Starting date	Duration (weeks)	Treatment type
1987	1	none	—	control
	2	July 7	2	early SD
	3	July 7	4	early SD
	4	July 7	2	early SD + DR
	5	July 7	4	early SD + DR
	6	July 21	2	mid-SD
	7	July 21	4	mid-SD
	8	July 21	2	mid-SD + DR
	9	July 21	4	mid-SD + DR
	10	Aug 4	2	late SD
	11	Aug 4	4	late SD
	12	Aug 4	2	late SD + DR
	13	Aug 4	4	late SD + DR
	14	Aug 18	2	late DR
1988	1	none	—	control
	2	June 30	2	early SD
	3	June 30	2	early DR
	4	June 30	2	late SD + DR
	5	July 15	2	late SD
	6	July 15	2	late SD + DR

Note: control = no short day and no drought
SD = short day
DR = drought
SD + DR = combined application of short day and drought

2.3 Sampling and Measurements

From May 5, 1987, until treatments began, 20 seedlings were randomly collected every 2 weeks from the control styroblocks. During treatments, 20 seedlings per treatment were collected weekly at random. End of season sample sizes are shown in Tables 2–3.

Shoot tips with unextended leaves were excised at the time of collecting and fixed immediately in McClintock's fixative (Johansen 1940). Shoot tips were later dissected and apical height and width (dimensions of the apical dome above the most recently initiated leaf primordium) were measured under a compound microscope. Apices were then hydrolysed in 1N HCl overnight, stained with Schiff's reagent (Feulgen reaction), and squashed (modified from Jensen 1962) to determine the mitotic index (MI) (number of dividing cells/total number of cells x 100).

In November 1988, 100 seedlings per treatment were randomly collected for morphological measurements. Also, 15 shoot tips per treatment were collected weekly between mid-October and early December for MI determination.

Shoot length of each seedling was measured from cotyledons to the base of unextended leaves. Root collar diameter was measured with a digital caliper. Juvenile leaf whorls and pairs of decussate leaves on the leader, and number of lateral shoots, were counted. Roots were carefully washed and separated from the shoots above the root collar. Shoots and roots were dried for 3 days at 70°C in a forced air convection oven and their dry weights determined.

TABLE 2. Dunnett's test comparisons of treatment means of shoot length (SHL), stem unit number (NSU), average stem unit length (SUL), root collar diameter (RCD), shoot and root dry weights (SDW and RDW, respectively) to the means of untreated (control) seedlings for the 1987 experiment

Variable:	SHL (mm)	NSU	SUL (mm)	SDW (g)	RCD (mm)	RDW (g)
n	60	60	60	40	80	40
Mean of the control (y)	221.3	41.47	5.34	1.0651	2.101	0.6900
Critical difference (y - y')	±16.8	±2.07	±0.32	±0.2216	±0.132	±0.1352
			Treatment differences (y - y')			
SD:						
early 2 wk	+8.1NS	-1.89NS	+0.45*	+0.1900NS	+0.209*	+0.1089NS
early 4 wk	-5.4NS	-0.40NS	-0.08NS	+0.1167NS	+0.163*	+0.0227NS
mid 2 wk	+12.47NS	+0.31NS	+0.25NS	+0.2161NS	+0.196*	+0.0226NS
mid 4 wk	-19.88*	-2.87*	-0.12NS	-0.1224NS	+0.024NS	+0.0066NS
late 2 wk	+27.00*	+0.90NS	+0.52*	+0.1600NS	+0.178*	-0.0129NS
late 4 wk	+16.10NS	-0.75NS	+0.49*	+0.2930*	+0.264*	+0.0060NS
SD+DR:						
early 2 wk	-31.9*	-2.29*	-0.51*	-0.0144NS	+0.011NS	-0.0226NS
early 4 wk	-41.1*	-3.00*	-0.66*	-0.1395NS	-0.040NS	-0.0665NS
mid 2 wk	-18.4*	-1.85NS	-0.16NS	-0.1224NS	+0.292*	+0.1257NS
mid 4 wk	-26.0*	-2.47NS	-0.33*	-0.0646NS	+0.022NS	-0.1221NS
late 2 wk	-29.6*	-3.12*	-0.34*	-0.1162NS	+0.045NS	+0.0181NS
late 4 wk	-34.9*	-3.10*	-0.48*	-0.1343NS	+0.076NS	-0.0327NS
DR						
Aug 2 wk	-0.1NS	-1.49NS	+0.19NS	+0.1061NS	-0.039NS	+0.0160NS
MS ERR	1083.64	16.5271	0.52726	0.125695	0.08898	0.046795

Note: (*) significant at $\alpha = 0.05$; $k = 14$, $df_{err} = \infty$

TABLE 3. Dunnett's test comparisons of treatment means of shoot length (SHL), stem unit number (NSU), average stem unit length (SUL), root collar diameter (RCD), shoot and root dry weights (SDW and RDW, respectively) to the means of untreated (control) seedlings for the 1988 experiment

Variable:	SHL (mm	NSU NR	SUL (mm)	SDW (g)	RCD (dm	RDW (g)
Mean of the control (y)	199.4	46.79	4.26	0.908	2.029	0.4682
Critical difference	±12.1	±1.59	±0.19	±0.080	±0.078	±0.0441
			Treatment differences (y - y')			
SD:						
early	-12.1*	+2.53*	-0.47*	-0.148*	+0.114*	-0.0504*
late	+15.5*	+3.68*	-0.01NS	+0.068NS	+0.099*	-0.0360NS
DR:						
early	+2.9NS	+1.41NS	-0.06NS	+0.012NS	+0.049NS	-0.0204NS
late	-10.1NS	+3.74*	-0.51*	+0.092*	+0.157*	+0.0047NS
SD+DR:						
early	-21.4*	+0.83NS	-0.52*	-0.154*	+0.087NS	-0.0436NS
late	-10.0NS	+3.35NS	-0.49*	-0.092*	-0.009NS	-0.0598*
MS ERR	1115.34	19.0401	0.2877	0.0481	0.0456	0.0147

Note: Sample size (n) = 100 for all treatments and variables; (*) significant at $\alpha = 0.05$, $k = 7$, $df_{err} = \infty$

Samples of cotyledons, whorled and decussate leaves, and dissected apices at different developmental stages were viewed under a scanning electron microscope. Leaves of DR and ND seedlings collected from various positions on the stem were also viewed. The specimens were gold-coated without any prior fixation, except shoot apices which were viewed without gold coating. Leaf stomatal distribution and configuration of epicuticular waxes were also determined.

2.4 Seedling Status Determination

Three 2-week trials were made to evaluate seedling status in the winter (December 20, 1988, and January 20 and February 20, 1989). On these dates, seedlings were placed in growth chambers at 20°C 8- and 16-h photoperiods, with a light intensity of 380 $\mu mol\ sec^{-1}\ m^{-2}$ for the duration of the experiments. Seedling dormancy status was determined by the resumption of mitotic activity in terminal and lateral apices and by shoot extension. Root growth potential (RGP) was determined by the increase in root volume and the number of white roots.

On December 16, 1988, several styroblocks containing control seedlings were placed in a growth chamber at +2°C 8-h photoperiod, with a light intensity of 380 $\mu mol\ sec^{-1}\ m^{-2}$. On each starting date, 48 seedlings were randomly selected, roots were carefully washed, root volume was measured, and the number of white roots were counted. Shoot length was measured and the lowest unextended leaves were marked with india ink. Six seedlings per pot were placed in 1-gallon pots containing a mixture of 3:3:1 peat moss, vermiculite, and sand. Four pots (24 seedlings) were placed at 20°C for a 16-h photoperiod. Another 24 seedlings were placed in a growth chamber at 20°C but for a 8-h photoperiod. A full styroblock with seedlings was also placed in each of these chambers. The seedlings were watered to saturation at the beginning and then every second morning.

Eight seedlings were collected daily (at noon) from styroblocks in each of the two 20°C chambers and their MI determined for one terminal and one lateral apex until mitotic divisions were found in the apices or until the end of the 2-week test period. Controls were collected from the +2°C chamber at the beginning and the end of each 2-week period. After 2 weeks, seedlings were removed from all pots, roots were carefully washed, and root and shoot measurements were repeated exactly as at the beginning of the experiments.

2.5 Outplanting

The 14 nursery treatments from 1987 were all outplanted in raised wet and dry farm-field beds at the Harmac (Nanaimo, B.C.) test site (Hawkins 1989).

All 1988 nursery treatments, except SD plus DR applied on June 30 (treatment No. 4, Table 1), were either placed in cold storage at +2°C on December 5, 1988, or planted into wet and dry raised beds at the Harmac site. For this planting, the wet and dry beds are defined by soil moisture tension as follows:

- wet – 0.1 ± 0.05 MPa before July 1 and 0.3 ± 0.05 MPa after that date; and
- dry – 0.5 ± 0.05 MPa before July 1 and 1.5 ± 0.05 MPa after that date.

From November through to the end of February (the wet season on eastern Vancouver Island dry sites), both bed types were exposed to ambient precipitation.

2.6 Frost Hardiness Assessments

During the fall of 1988, and before planting in December 1988 and April 1989, all treatments except No. 4 were assessed for foliage frost hardiness under standard B.C. Forest Service, Silviculture Branch, test conditions.

2.7 Data Analyses

Treatment means were compared to the control mean by Dunnett's test. In 1988, the data were also analyzed by ANOVA contrasts. Percentage data were transformed using arcsine transformation and multiple comparison of proportions was done using Tukey-type multiple comparison test for proportions (Zar 1984).

The field data were reduced to replicate means and analyzed with a split plot ANOVA. Beds (B) and replicates (R) are considered random, while nursery treatments (N) and storage durations (S) are considered fixed factors in the ANOVA model. Analyses were deemed significant at $\alpha = 0.05$.

3 RESULTS AND OBSERVATIONS

3.1 Growth Pattern of Untreated Seedlings

The period of germination was from 7 to 30 days after sowing. Two cotyledons emerged carrying a seedcoat (Plate 1). A pair of true leaves then appeared at right angles to cotyledons (Plate 5). The next leaves were initiated as whorls of four (Plate 6), and then usually in whorls of three (Plate 7). Transition to the initiation of decussate leaves on the leader (Plate 8) began during late summer, although about half of the seedlings entered dormancy without undergoing this transition. The first lateral shoots appeared in May bearing the decussate scale-like foliage. A damaged terminal apex was usually replaced by the closest lateral, and the leader from that point on had decussate scale-like leaves.

The number of internodes (whorls or pairs of leaves) on the leader increased rapidly in May and June. Initiation of new stem units slowed in July, increased again in August, and then continued at a moderate rate through September before stopping in early October (Figure 3). This corresponds to changes in the MI.

Generally, there were two major and a minor peak in MI (Figure 3). Mitotic index was high in May, decreased in June, and increased again in late July, reaching the second major peak in early August. It then declined steadily until the end of August, and briefly increased in mid-September after which it declined to zero (December 1987; end of November in 1988). This is the time when seedlings were considered to be dormant.

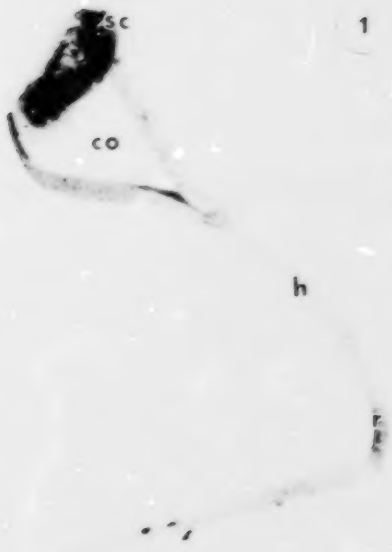
The apical height and width were maximum in mid-summer, 0.45 ± 0.01 and 0.64 ± 0.01 mm, respectively. Apical dimensions declined in the fall reaching their minimum when MI became zero.

PLATE 1. A germinant with two cotyledons (co) carrying a seedcoat (sc), the hypocotyl (h), and radicle (r). X 5

PLATE 2. Young seedlings in mid-June, about 2 months after germination. Root system is weak, the radicle-originated root (arrow) is the largest, and only a few lateral roots have been initiated. Three to four lateral shoots (ls) have been already initiated and some have extended. X 0.42

PLATE 3. Randomly selected seedlings from the control group (C) and the early July, 2-week treatments of (A) short day (SD), and (B) SD x drought (DR). Reduced height is obvious in the SD x DR treatment. Roots within all groups have become more massive than in the previous figure and the typical fibrous root system is present. X 0.35

PLATE 4. Randomly selected seedlings from the control group (C) and the late July, 4-week treatments of (A) SD, and (B) SD x DR. There are no morphological differences between the SD seedling and the control seedling. X 0.30



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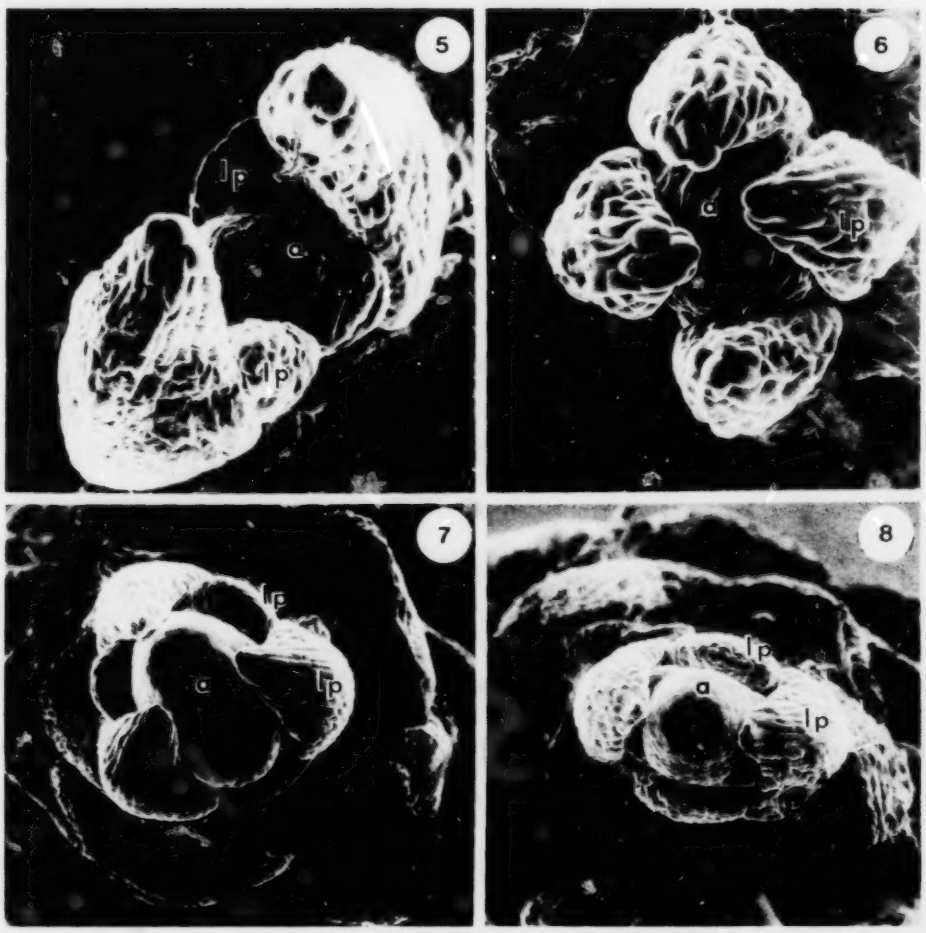


PLATE 5. Shoot apex (a) shortly after germination. Cotyledons were removed. A pair of enlarged leaves (arrows) was initiated first and then a whorl of four leaf primordia (lp). X 180

PLATE 6. A whorl of four slightly elongated juvenile-type leaf primordia during early seedling development. X 220

PLATE 7. Whorls of three leaves were most commonly initiated before the transition to the initiation of mature decussate leaves. Alternating whorls were positioned at a 60° angle to each other. X 140

PLATE 8. Mature, decussate leaf primordia were initiated at a 90° angle to each other. X 110

The most rapid height growth occurred between early June and mid-July (Figure 4) and then slowed until dormancy. Root collar diameter (Figure 4) increased quickly in May and early June and then slowed and stopped in August. Shoot dry weight (Figure 5) increased slowly until mid-June and then rapidly until September. Lateral shoots were initiated most rapidly in June and early July. After mid-September, initiation was minimal.

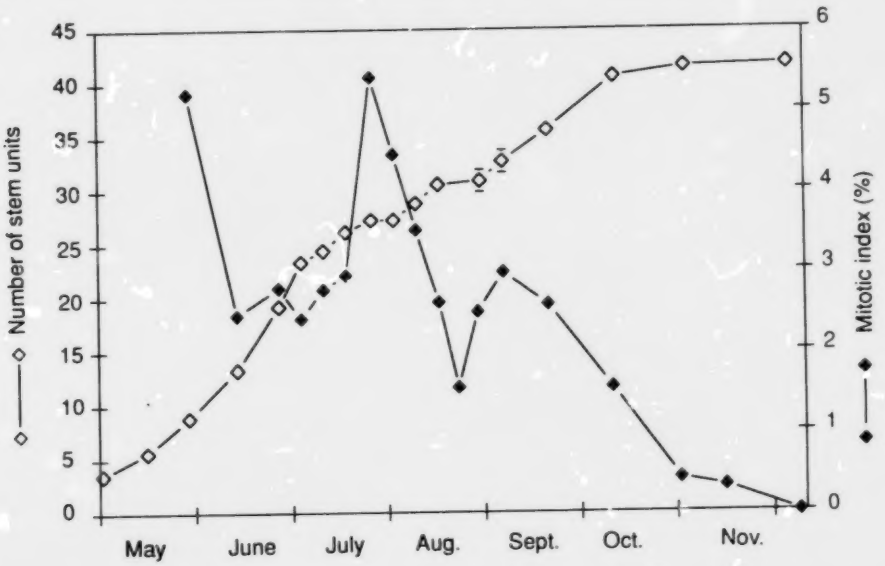


FIGURE 3. Number of stem units (NSU) and apical mitotic index (MI) of the untreated (control) seedlings versus time in monthly intervals. Note: Collections of 20 seedlings per date were obtained from May 5 for measurements of stem unit number, and from May 20 for mitotic index.

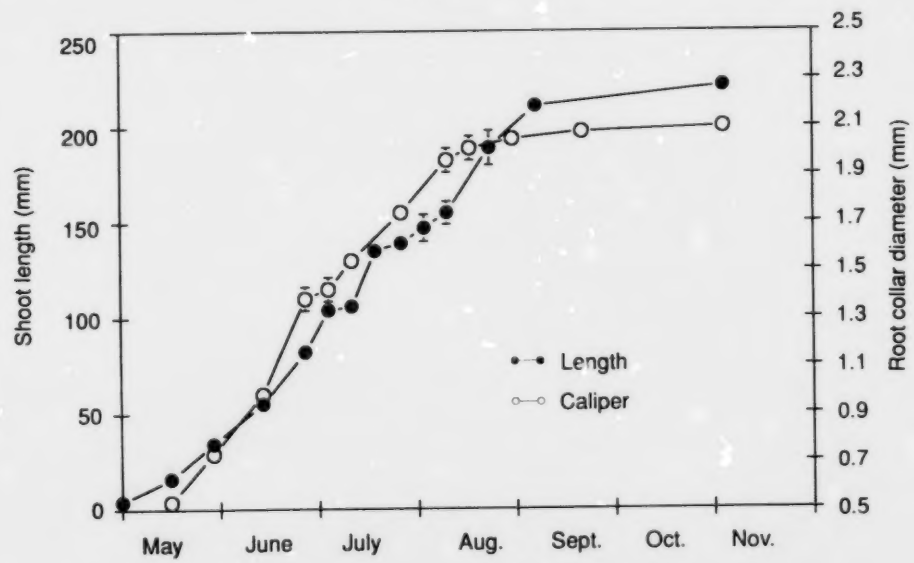


FIGURE 4. Stem length and root collar diameter (caliper) in the untreated (control) seedlings versus time in monthly intervals. Note: Collections of 20 seedlings per date were obtained from May 20 until the end of the growing season.

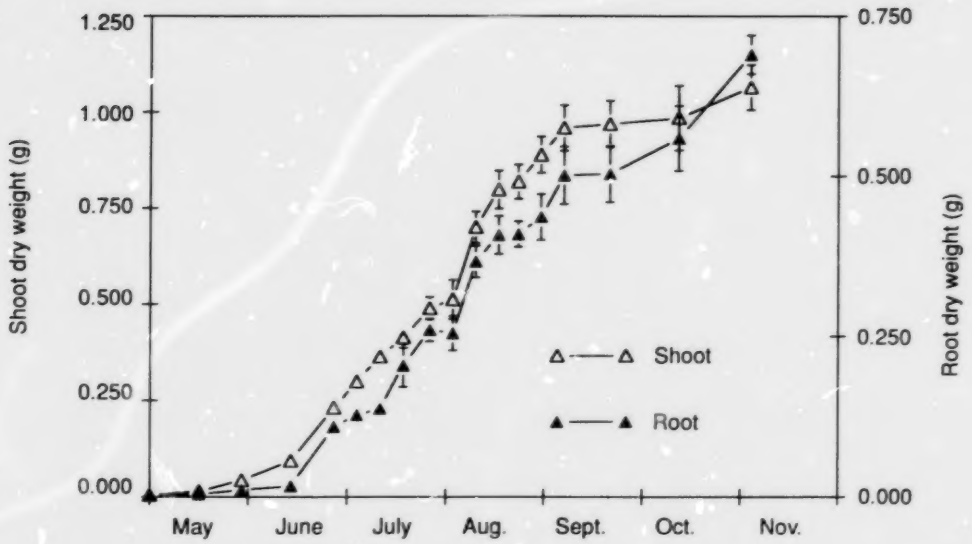


FIGURE 5. Shoot and root dry weights of the untreated (control) seedlings versus time in monthly intervals. Note: Collections of 20 seedlings per date were obtained from May 20 until the end of the growing season.

The increases in root dry weight were cyclic and very slow during early growth (Figure 5). Until mid-June, the root system consisted mainly of the primary root (Plate 2). The fibrous root system, typical for western redcedar, had not yet developed. In mid-June, more roots were initiated and root dry weight increased rapidly. Lateral roots then increased in length and thickness, forming a fibrous root system in most seedlings by mid-July (Plate 3). Root growth ceased in November.

3.2 The Influence of Treatments on Seedling Morphology

It was determined that average daily temperatures were often slightly higher in the blackout greenhouse than in the ambient one (Figures 1-2).

3.2.1 Height, shoot length components, root collar diameter, shoot and root dry weights

1987 experiment:

Treatments consisting of a combination of short day and moisture stress (SD + DR) reduced the final seedling height (Table 2, Figure 6). Although 4-week treatments resulted in greater reduction of the final height than the 2-week ones, the differences were not proportional to the prolonged treatment duration. Elongation of the leader was usually suppressed during the time of treatment application (Figures 8 A, B). Seedlings from 4-week durations continued to extend their leaders at significant rates for two weeks longer than the 2-week treated seedlings (Figures 8 A, B) and the controls. All SD + DR treatments reduced the number (Table 2, Figure 9) and average length of stem units (Table 2), but it was the latter that significantly reduced seedling height. SD + DR treatments produced seedlings with smaller final shoot dry weights than in the untreated controls (Table 2, Figure 11). SD + DR treatments slightly increased root collar diameter compared to untreated seedlings (Table 2, Figure 13) but did not significantly affect root dry weight (Table 2, Figure 11).

The effects of short days (SD) applied without simultaneous moisture stress (DR) were less consistent than the effects of the SD + DR treatments. The only significant height reduction occurred in the 4-week, mid-July treatment (Table 2, Figure 6) and resulted mainly from a decreased number of stem units (Table 2, Figure 9). All other SD treatments either had no significant effect on height (particularly early treatments) or increased height (late treatments). Treatments that increased height did so by significantly

increasing the average length of stem units rather than their number (Table 2). Mean shoot dry weights of seedlings treated with SD only were usually higher than in the controls (Table 2, Figure 11). Also, root collar diameters in seedlings treated with SD only were usually greater than in the untreated controls (Table 2, Figure 13) but root dry weights were not significantly different (Table 2, Figure 11). When DR alone was applied for 2 weeks in mid-August, the treated seedlings reached their maximum root dry weight about a month earlier than the controls but the final weights of controls and the treated seedlings were about the same (Figure 15).

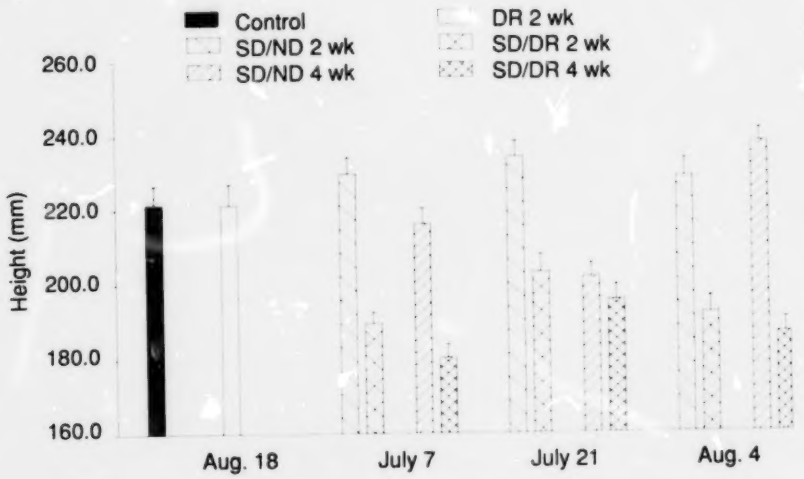


FIGURE 6. Final height of seedlings from 1987 growing season. The means are based on 60 seedlings per treatment combination. Note: AD, SD, DR, ND indicate ambient day, short day, drought, and no drought, respectively, lasting 2 weeks (2 wk) and 4 weeks (4 wk).

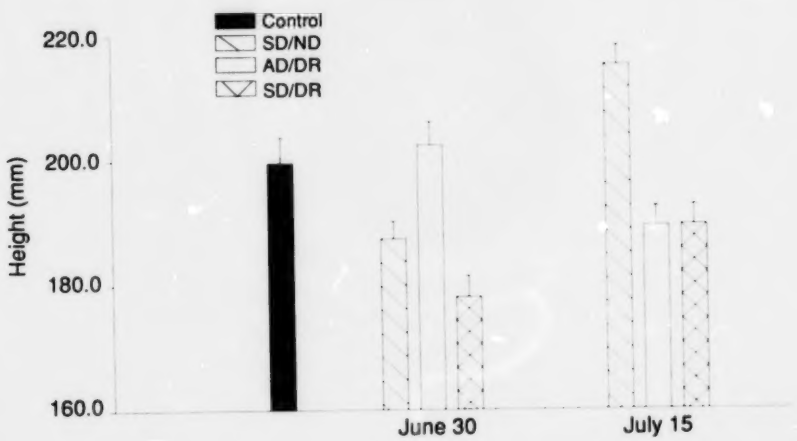


FIGURE 7. Final height of seedlings from 1988 growing season. All treatments lasted 2 weeks. The means are based on 100 seedlings per treatment combination.

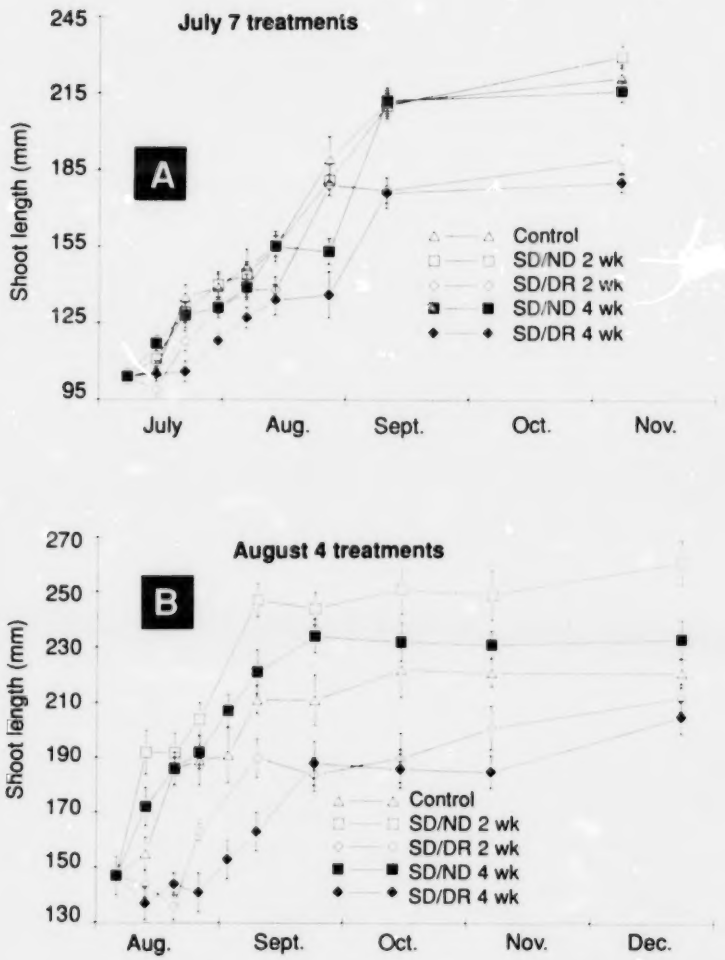


FIGURE 8. Height increases in the untreated (control) seedlings and treated seedlings versus time. Treatments began on July 7 (A), and August 4 (B), 1987. Note: Collections of 20 seedlings per date were obtained from July 7, until the end of the growing season. SD, ND, SD/DR indicate short day, no drought, and short day plus drought lasting 2 weeks (2 wk) and 4 weeks (4 wk).

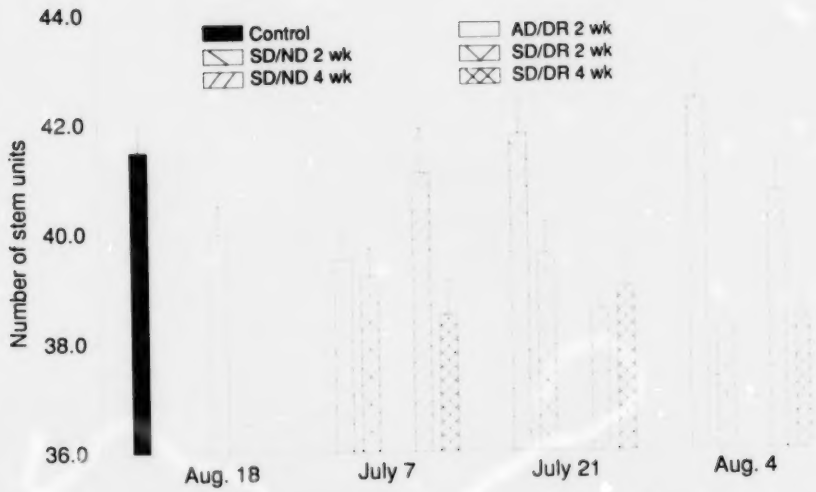


FIGURE 9. Final number of stem units in seedlings from 1987 growing season. The means are based on 60 seedlings per treatment combination. Note: AD, SD, DR, ND indicate ambient day, short day, drought, and no drought, respectively, lasting 2 weeks (2 wk) and 4 weeks (4 wk).

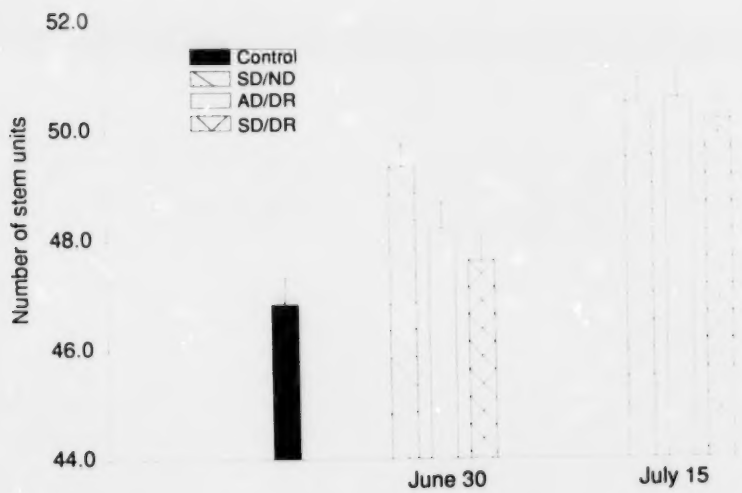


FIGURE 10. Final number of stem units in seedlings from 1988 growing season. All treatments lasted 2 weeks. The means are based on 100 seedlings per treatment combination.

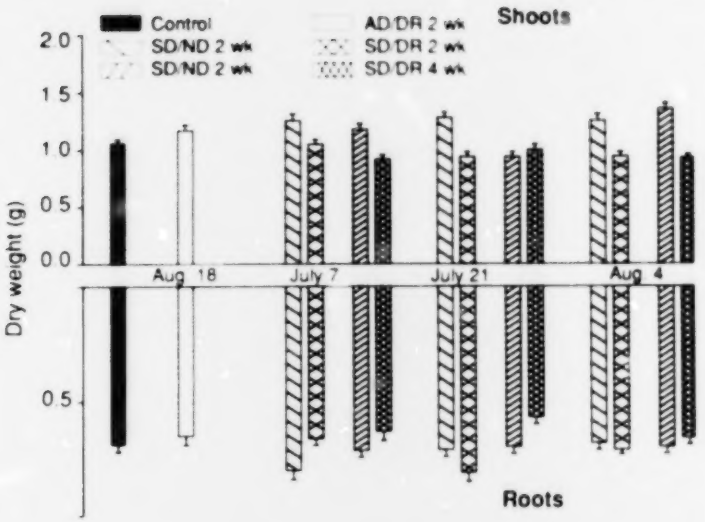


FIGURE 11. Final shoot and root dry weights in seedlings from 1987 growing season. The means are based on 40 seedlings per treatment combination for shoot and 40 seedlings for root dry weight. Note: AD, SD, DR, ND indicate ambient day, short day, drought, and no drought, respectively, lasting 2 weeks (2 wk) and 4 weeks (4 wk).

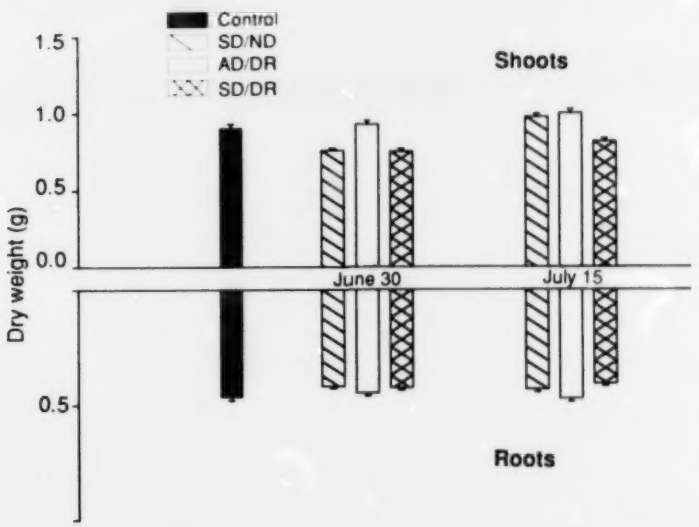


FIGURE 12. Final shoot and root dry weights in seedlings from 1988 growing season. All treatments lasted 2 weeks. The means are based on 100 seedlings per treatment combination.

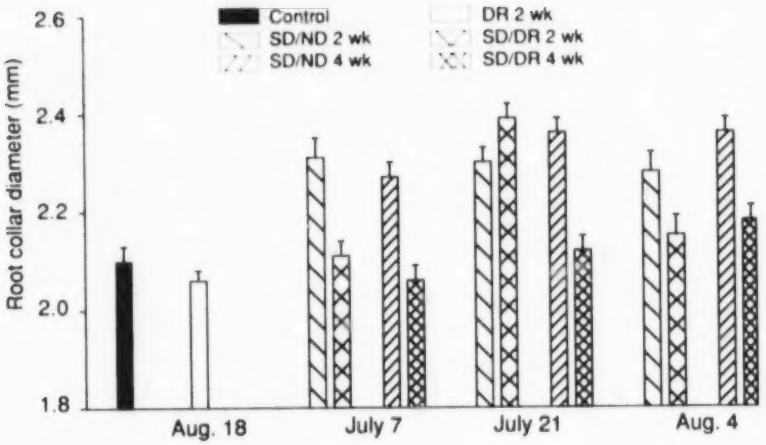


FIGURE 13. Final root collar diameter of seedlings from 1987 growing season. The means are based on 80 seedlings per treatment combination. Note: AD, SD, DR, ND indicate ambient day, short day, drought, and no drought, respectively, lasting 2 weeks (2 wk) and 4 weeks (4 wk).

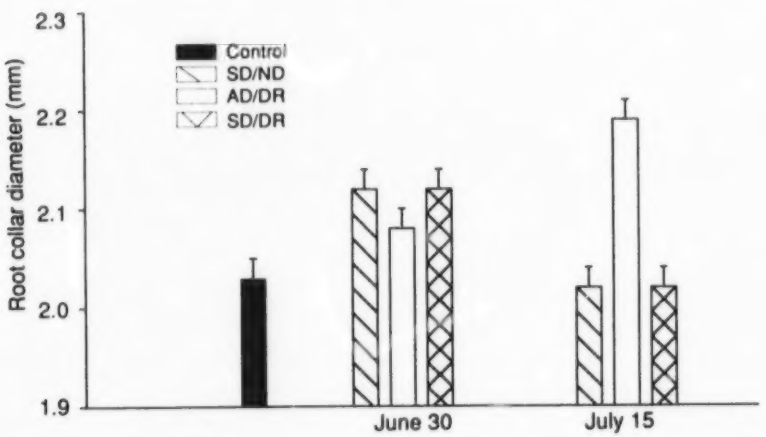


FIGURE 14. Final root collar diameter of seedlings from 1988 growing season. All treatments lasted 2 weeks. The means are based on 100 seedlings per treatment combination.

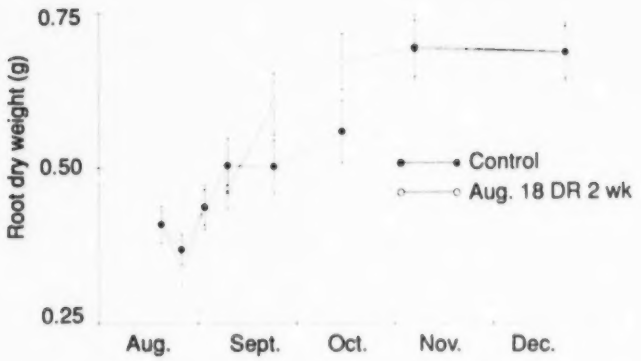


FIGURE 15. Root dry weight increase in the untreated (control) seedlings and those treated with drought on August 18, 1987, versus time. An enhancement of root dry weight by drought (DR) occurred shortly after termination of DR. Note: Collections of 20 seedlings per date were obtained from August 18, until the end of the growing season.

1988 experiment:

The only treatments that consistently reduced height were those involving the combination of short photoperiod and moisture stress (SD + DR) (Table 3, Figure 7). However, there were significant differences between the early and late SD + DR treatments in the magnitude of height reduction, number of stem units, and root collar diameters (Table 4). The early SD + DR treatment resulted in the greatest reduction in height and shoot dry weight of all the 1988 treatments without significantly affecting root collar, root dry weight and diameter (Table 3, Figures 12 and 14). The late SD + DR significantly reduced root dry weight in comparison to untreated seedlings (Table 3). Both early and late SD + DR significantly shortened the average stem unit length (Table 3).

The effects of short day (SD) and moisture stress (DR) applied separately depended on the time of treatment application (Table 4). Early SD significantly reduced height whereas the late SD significantly increased it (Table 3, Figure 12). Late SD had no effect on the stem unit length (Table 3) but increased stem unit number (Table 3, Figure 10). Moisture stress alone did not significantly alter seedling height (Table 3, Figure 12).

Generally, changes to root collar diameter and root dry weight brought about by separate applications of short days or moisture stress were of little practical importance. Mean root collar diameter was increased at statistically significant level by early and late SD treatments and by late DR (Table 3, Figure 14); however, the largest difference compared to untreated controls was only 7.7%.

3.2.2 Leaves and lateral shoots

The number of leaf whorls and decussate leaf pairs on the leader equals the NSU. Late June treatments resulted in initiation of fewer decussate leaves while July treatments did not significantly affect the initiation of decussate leaves (Table 5).

The SD with DR reduced the number of lateral shoots (Figures 16 and 17). When applied at the end of June, SD reduced the number of lateral shoots, whereas later applications had no significant effect (Figures 16 and 17).

3.2.3 Mitotic index

Treatments affected the MI of terminal shoot apices during application and shortly after but did not cause any differences in timing of cessation of mitotic activity in late fall (Figure 18). Treatment-specific data are not presented because the observed differences were inconsistent.

TABLE 4. Anova contrasts comparing the influence of the time of treatment application on shoot length, shoot dry weight, number of stem units (NSU), stem unit length (SUL), root collar diameter, and root dry weight

Source	df	SS	F	P>F	Proportion of treatment SS
		Var. Shoot Length			
Treatment	6	117927.82			
Contrast questions:					
SD early vs late	1	38364.50	28.17	0.00000	32.53
DR early vs late	1	7775.05	5.71	0.01713	6.59
SD+DR early vs late	1	6462.94	4.74	0.02970	5.48
Error	693	943618.21			
		Var. Shoot Dry Weight			
Treatment	6	6.024421			
SD early vs late	1	2.32180	42.21	0.00000	38.54
DR early vs late	1	0.31554	5.74	0.01688	5.24
SD+DR early vs late	1	0.11753	3.50	0.06162	3.20
Error	693	38.11553			
		Var. NSU			
Treatment	6	1333			
SD early vs late	1	66	2.91	0.08828	4.96
DR early vs late	1	271	11.96	0.00058	20.36
SD+DR early vs late	1	317	13.99	0.00020	23.81
Error	693	15727			
		Var. SUL			
Treatment	6	38.90			
SD early vs late	1	10.58	30.20	0.00000	27.20
DR early vs late	1	10.12	28.90	0.00000	26.03
SD+DR early vs late	1	0.05	0.13	0.72000	0.11
Error	693	242.75			
		Var. root collar diameter			
Treatment	6	2.21333			
SD early vs late	1	0.01110	0.21	0.64732	0.42
DR early vs late	1	0.58320	11.00	0.00096	22.25
SD+DR early vs late	1	0.46080	8.69	0.00330	17.57
Error	693	36.7236			
		Var. Root Dry weight			
Treatment	6	0.3718			
SD early vs late	1	0.0103	0.60	0.43816	2.78
DR early vs late	1	0.0314	1.83	0.17655	8.44
SD+DR early vs late	1	0.0131	0.77	0.38095	3.55
Error	693	11.90			

TABLE 5. Comparison of seedling proportions which underwent transition to initiation of decussate (mature) leaves on the leader in treated seedlings vs. the controls

Treatment type	Proportion of decussate leaves	
control	0.49	a
AD+DR July	0.51	a
SD+DR July	0.42	a
SD+ND July	0.36	a
SD+ND June	0.31	b
AD+DR June	0.28	b
SD+DR June	0.23	b

Note: Compared by Tukey-type multiple comparison for proportions (Zar 1984). Values followed by the same letter are not statistically significant ($p > 0.005$). AD – ambient day length, SD – short day, DR – drought stress, ND – no drought stress.

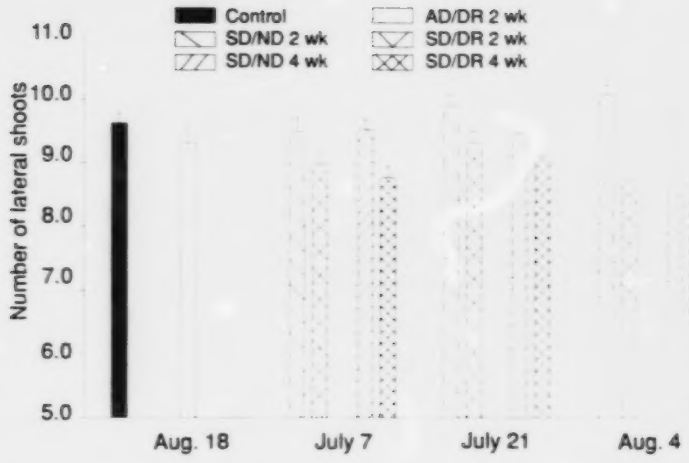


FIGURE 16. Final number of primary lateral shoots in seedlings from 1987 growing season. The means are based on 60 seedlings per treatment combination. Note: AD, SD, DR, SD/DR indicate ambient day, short day, drought, and short day plus drought, respectively, lasting 2 weeks (2 wk) and 4 weeks (4 wk).

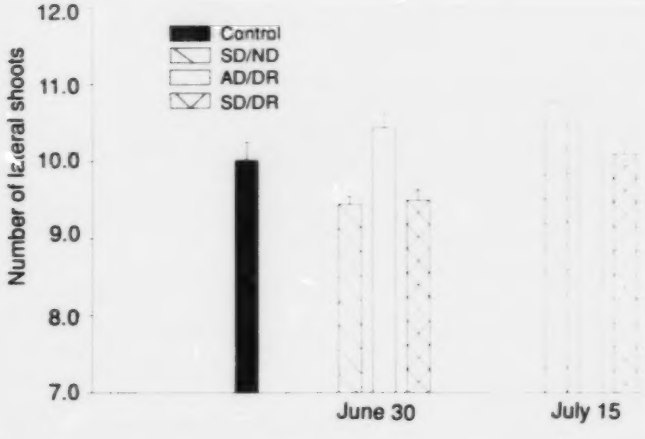


FIGURE 17. Final number of primary lateral shoots in seedlings from 1988 growing season. All treatments lasted 2 weeks. The means are based on 100 seedlings per treatment combination.

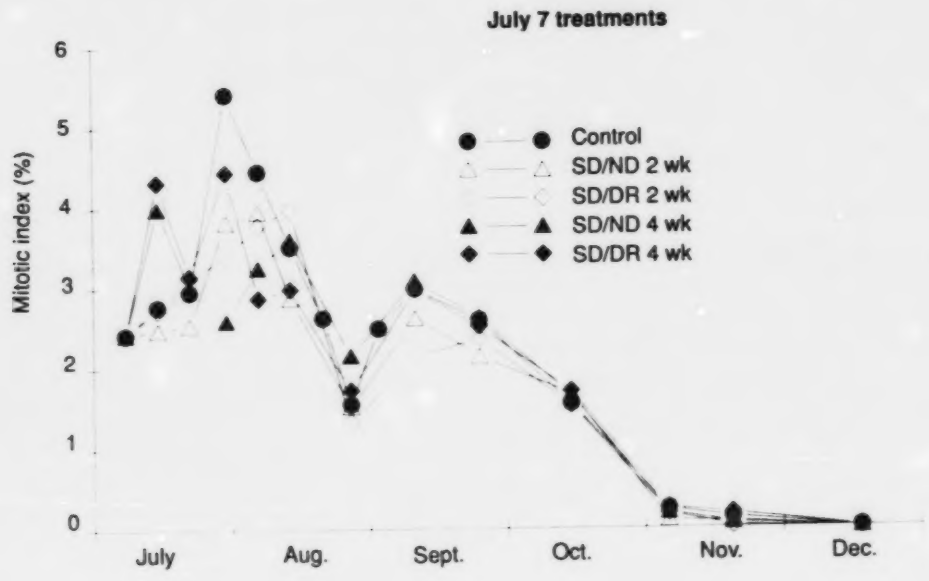


FIGURE 18. Mitotic indices of the untreated (control) and treated seedlings versus time. Treatments began on July 7, 1987, and lasted 2 and 4 weeks (2 wk and 4 wk), respectively. Seedlings from all treatment combinations ceased mitotic activity at about the same time. Note: Collections of 20 seedlings per date were obtained from July 7 until mid-December. SD, DR, SD/DR indicate short day, drought, and short day plus drought, respectively.

3.2.4 Stomata distribution and epicuticular waxes

The abaxial and adaxial surfaces of cotyledons were ribbed and lacked the minute glands (Plate 9) which were observed on surfaces of true leaves (Plate 10). Gland arrangement was more regular in juvenile leaves (Plates 10-14). Rows of stomata occurred on the adaxial surface but were absent on the abaxial surface of cotyledons (Plate 9). True leaves had stomata arranged in a strip on either side of the midrib on both surfaces, with most occurring on the abaxial surface (Plates 10–14). Juvenile awl-shaped leaves had very few rows of stomata on the adaxial surface and abundant stomata distributed irregularly within a strip on either side of the midrib on the adaxial surface (Plate 11). Most stomata were not plugged by waxes (Plates 14 and 19). Clumps of wax (Plate 20) and fine hairy plugs (Plate 21) were occasionally observed within the stomatal orifice of stressed and untreated seedlings.

Both surfaces of true leaves, including margins and midribs, were covered with epicuticular waxes, usually as fine intermeshed rods (Plates 15–22). These rods covered guard cells and glands on the abaxial surface (Plates 18 and 19) but not the glands on the adaxial surface (Plates 15 and 16).

Generally, there were very few differences in wax configuration between the treated and untreated seedlings. There was a greater abundance of thick crusts and clumps of wax (Plates 22 and 23) on the leaves of drought stressed seedlings, particularly those apparently initiated during and after drought stress.

PLATE 9. The abaxial surface of a cotyledon is free of stomata. X 550

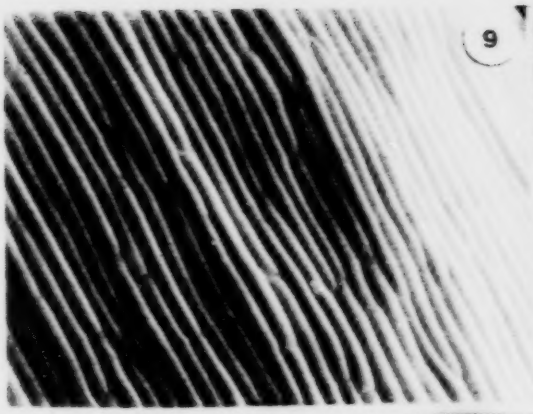
PLATE 10. The adaxial surface of a juvenile leaf with few rows of stomata (arrows) and numerous minute glands (gl) arranged into rows. X 120

PLATE 11. The abaxial surface of a juvenile leaf with numerous stomata irregularly arranged on either side of the midrib (mr). X 75

PLATE 12. The adaxial surface of a mature leaf. Stomata are not abundant and are irregularly arranged on either side of the midrib. X 40

PLATE 13. The abaxial surface of a mature leaf with numerous irregularly arranged stomata on either side of the midrib but occasionally also on the midrib (arrow). X 80

PLATE 14. A higher magnification of the abaxial surface of a mature leaf as in Plate 13 showing abundant open stomata and many minute glands. X 150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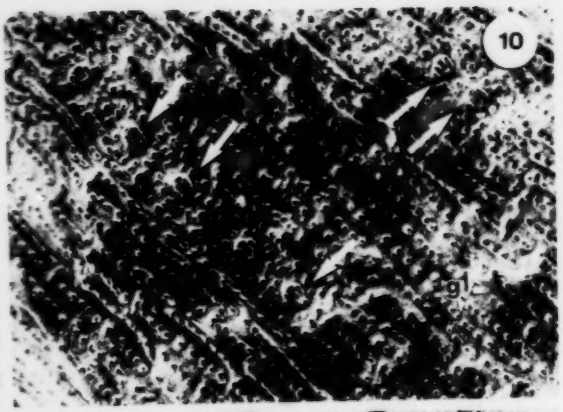
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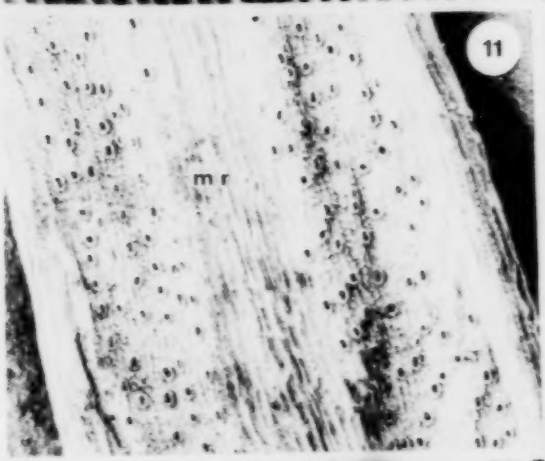
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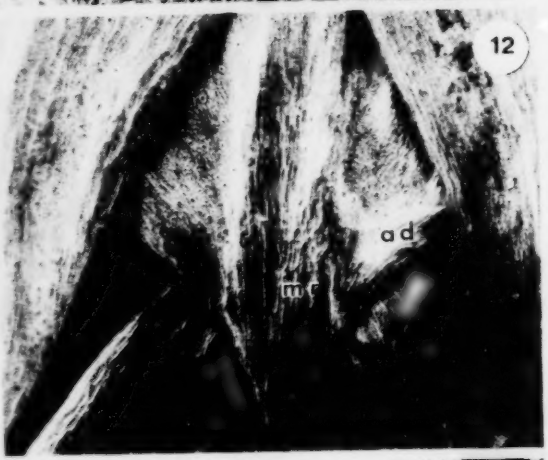
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ad
mr

13
mr

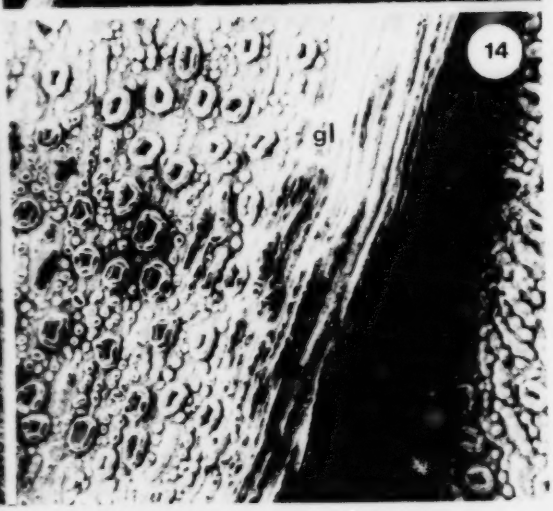

14
gl

PLATE 15. The adaxial surface of a juvenile leaf from a control seedling group showing fuzzy layer of wax (w) and protruding minute glands (gl). X 950

PLATE 16. Higher magnification of the area shown in Plate 15 showing crumbled wax (cw) around the glands. X 1200

PLATE 17. Ribbed leaf margin of a mature leaf, from a control seedling covered with abundant intermeshing wax. X 1500

PLATE 18. The abaxial surface of a mature leaf, from a control seedling, covered with a layer of fine intermeshing wax including surfaces of guard cells (gc) and glands. X 800

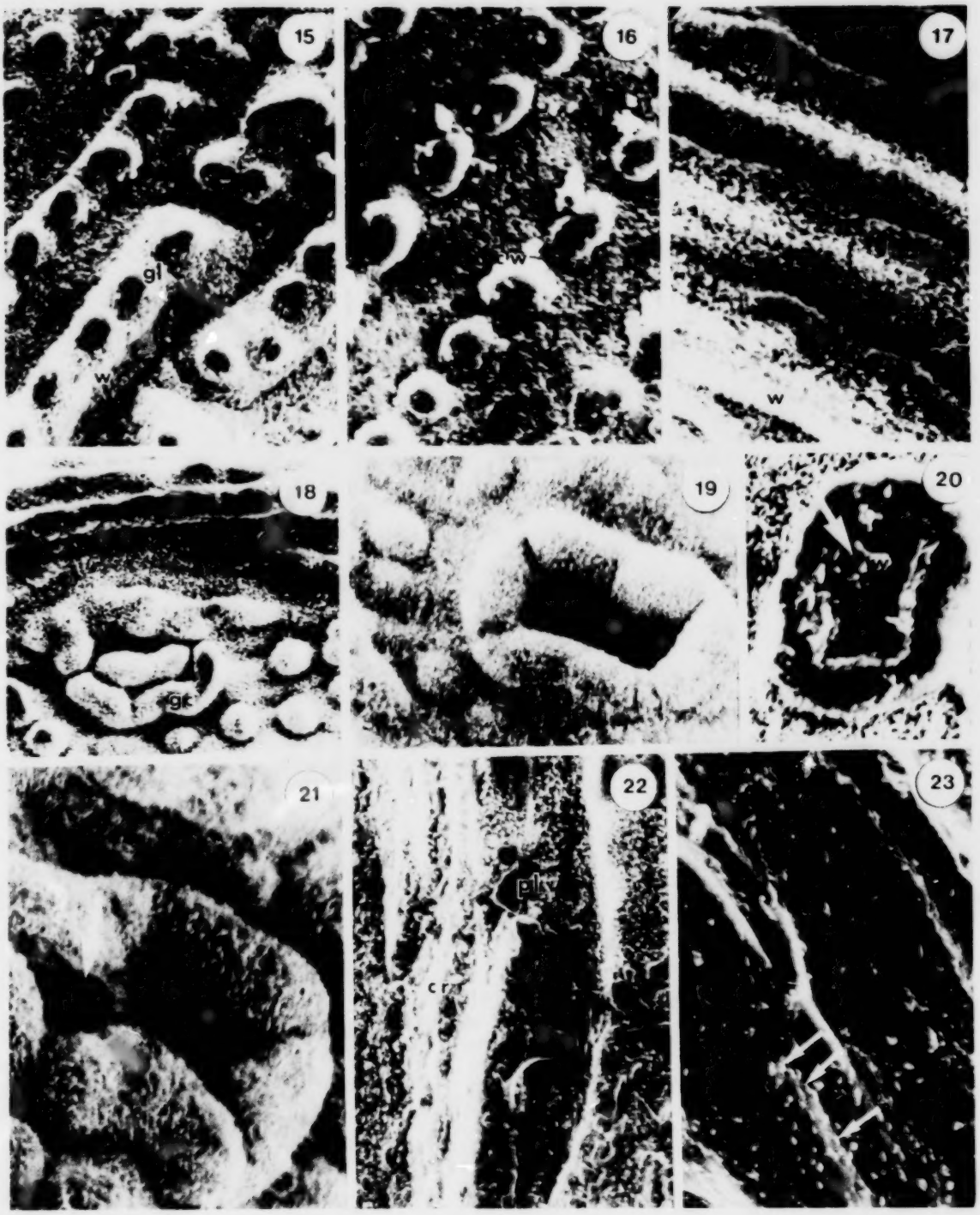
PLATE 19. An open stoma on the abaxial surface of a mature leaf, of a control seedling, with no stomatal plug. X 1600

PLATE 20. An open stoma with a partial wax plug (arrow) of amorphous wax on the abaxial surface of a mature leaf from a control seedling. X 1600

PLATE 21. Partially plugged stoma (arrow) on the abaxial surface of a mature leaf of a drought-stressed seedling. X 8500

PLATE 22. Plates (pl) and crusts (cr) of amorphous wax on the abaxial surface of a mature leaf from a drought-stressed seedling. X 650

PLATE 23. Ribbed mature leaf margin covered with a solid layer of amorphous wax with abundant granular protrusions (arrow) from a drought-stressed seedling. X 1800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3.2.5 Dormancy release and root growth potential

Shoot and root growth of western redcedar seedlings could be evoked during winter by placing seedlings in favourable growth conditions of 20°C and either 8- or 16-h photoperiods. The promptness and degree of observed responses differed depending on the time of placing seedlings in favourable conditions. Shoot apices resumed mitoses most slowly when placed in favourable growth conditions in December. Generally, resumption of mitotic activity was faster under a 16- than 8-h photoperiod (Table 6). In December, terminal apices of seedlings under 20°C 8-h photoperiods remained mitotically inactive for 11 days; under 16-h photoperiod mitotic activity began after only 4 days. Such difference became less in January and February experiments where mitotic activity of terminal apices was resumed 1 day earlier in seedlings kept under 16-h photoperiod. In January, terminal apices resumed mitoses more promptly than lateral apices. Interestingly, the first mitoses were often followed by a short period of lower or no mitotic activity (Table 6).

Measurable growth of shoots (Table 7A) reflected the observed pattern of resumption of mitotic activity. Height increase during the 2-week durations of the trials was always much greater under 16- than 8-h photoperiods. By February, height increase under 8-h photoperiods was much greater than that observed in January or December.

Roots differed from shoots in their response to favourable growth conditions (Table 7B). The greatest increase in root volume and the number of white roots occurred in December (Table 7A). Root growth was also good in February. The number of new white roots was remarkably low in January under both photoperiods, whereas shoots grew well at that time under 16-h photoperiods and better than in December under 8-h photoperiods (Table 7A).

3.2.6 Frost hardiness and field performance

Only the 1988/89 outplanting results are reported here. (See Hawkins (1989) for the 1987/88 outplanting results).

At lifting in December, both DR nursery treatments (Nos. 3 and 6; Tables 1 and 8) had the least resistance to low temperature exposure (Table 8). There was very little difference in frost resistance between the other treatments at this time, a range of only 1.5°C. After cold storage, the range over all nursery treatments was 2°C for the LT25. The two DR treatments increased in resistance during storage while the other treatments decreased (Table 8).

At planting, height and root collar diameter (RCD) were significantly different between nursery treatments, but not for any other factor in the mixed model ANOVA. The range of means at planting was 4.7 cm and 0.3 mm for height and RCD, respectively. By September when the fall assessment was conducted, survival was near 100% for all treatments, regardless of storage or bed type. Height was significantly affected by bed type and nursery treatment; RCD was not affected by any factor in the model (Table 9). Even though first-year height was significantly affected by nursery treatment, the differences were minimal (Table 10). Seedlings planted in dry beds were significantly shorter than those planted in wet beds (Table 9), 33.7 versus 37.3 cm, a mean range of 3.6 cm. The nursery treatment range in mean heights at the fall measurement was 3.4 cm versus 4.7 cm at planting.

Height, RCD, and volume increments were all significantly affected by storage (Table 11). Non-stored seedlings gained 1.2 cm more height, 0.27 mm more RCD, and 0.44 cm^3 more volume during the 1989 season (Table 12). Height increment was also significantly affected by bed type, with wet bed planted seedlings accruing 3.4 cm more height than dry bed planted (Table 12). There was also an interaction between storage and nursery treatment for volume increment (Table 11), attributable to different nursery treatment rankings between stored and non-stored stock.

TABLE 6. Number of mitotically active apices (AA) and the mitotic index in dormancy release trials at 20°C and two different photoperiods

Starting date	Days from start	Terminal apices				Lateral apices			
		8 hr AA	MI	16 h AA	MI	8 h AA	MI	16 h AA	MI
Dec. 20	1	0/8	0	0/8	0	0/8	0	0/8	0
	2	0/8	0	0/8	0	0/8	0	0/8	0
	3	0/8	0	0/8	0	2/8	0.3%	2/8	1.2%
	4	0/8	0	4/8	1.1%	2/8	0.6%	5/8	0.9%
	5	0/8	0	8/8	1.3%	3/8	1.0%	8/8	2.3%
	6	0/8	0	*	*	5/8	1.3%	*	*
	7	0/8	0	*	*	*	*	*	*
	8	0/8	0	*	*	*	*	*	*
	9	0/8	0	*	*	*	*	*	*
	10	0/8	0	*	*	*	*	*	*
	11	0/8	0	*	*	*	*	*	*
	12	1/8	0.7%	*	*	*	*	*	*
	13	0/8	0	*	*	*	*	*	*
	14	2/8	0.5%	*	*	*	*	*	*
Jan. 20	1	0/8	0	0/8	0	0/8	0	0/8	0
	2	0/8	0	3/8	0.1%	0/8	0	1/8	0.2%
	3	3/8	0.3%	5/8	0.6%	0/8	0	0/8	0
	4	0/8	0	8/8	0.6%	3/8	1.0%	7/8	1.7%
	5	0/8	0	*	*	0/8	0	6/8	1.1%
	6	6/8	0.6%	*	*	0/8	0	*	*
	7	5/8	1.6%	*	*	6/8	1.3%	*	*
	8	*	*	*	*	*	*	*	*
	9	*	*	*	*	*	*	*	*
	10	*	*	*	*	*	*	*	*
Feb. 20	1	0/8	0	0/8	0	0/8	0	8/8	1.8%
	2	0/8	0	2/8	0.5%	0/8	0	2/8	0.3%
	3	1/8	0.5%	8/8	0.7%	6/8	1.1%	8/8	2.1%
	4	6/8	1.0%	*	*	7/8	0.8%	*	*
	5	8/8	0.8%	*	*	8/8	1.2%	*	*
	6	*	*	*	*	*	*	*	*
	7	*	*	*	*	*	*	*	*
	8	*	*	*	*	*	*	*	*
	9	*	*	*	*	*	*	*	*
	10	*	*	*	*	*	*	*	*

* All active, the MI not determined.

TABLE 7A. Mean increases in height (H), root volume (RV), and the number of white roots (WhR) after 14 days at 20°C and 8- and 16-h photoperiods

Date of testing	N	8-h photoperiod			16-h photoperiod		
		H (mm)	RV (mm^3)	WhR	H (mm)	RV (mm^3)	WhR
Dec. 20	24	0.21	1.04	31.79	22.75	1.44	41.08
		±0.17	±0.14	±1.81	±1.40	±0.11	±2.91
Jan. 20	24	3.37	0.43	12.58	25.04	1.28	19.79
		±0.48	±0.10	±1.23	±1.18	±0.09	±1.65
Feb. 20	24	11.79	0.99	26.50	23.13	1.29	36.82
		±0.96	±0.11	±2.21	±1.54	±0.10	±3.15

TABLE 7B. Analysis of variance on mean increase in height (H), root volume (RV), and number of white roots (WhR) for western redcedar seedlings at 8- and 16-h photoperiods (PHOTO), 20°C, and three starting dates (START)

Variable	Source	df	SS	F	P
H					
	START	2	816.75	6.48	0.0001
	PHOTO	1	1232.22	453.85	0.0001
	START*PHOTO	5	918.50	16.92	0.0342
ERROR		137	3719.61		
RV					
	START	2	3.84	6.48	0.0020
	PHOTO	1	9.75	32.93	0.0001
	START*PHOTO	5	2.05	3.46	0.0342
ERROR		137	40.56		
WhR					
	START	2	10708.10	44.31	0.0001
	PHOTO	1	2851.80	23.60	0.0001
	START*PHOTO	5	60.00	0.25	0.7804
ERROR		137	16552.90		

Note: SS = sum of squares.

TABLE 8. Temperature which resulted in 25% (LT25) foliage browning (death) to western redcedar by nursery treatment under standard test conditions during the fall of 1988 and the spring of 1989

Test date	Nursery treatment[a]					
	1 Control	2 SD/ND June	3 AD/DR June	5 SD/ND July	6 AD/DR July	7 SD/DR1 July
20 Sept.	-10.5	-5.5	-5.0	-6.0	-5.5	-5.5
15 Nov.	-10.0	-9.5	-10.0	-10.0	-10.0	-10.0
05 Dec[b]	-15.0	-14.5	-10.0	-15.0	-10.0	-15.0
12 Apr[c]	-13.5	-12.0	-14.0	-14.0	-13.0	-12.5

[a] See Table 1 for legend.

[b] Time of lift.

[c] End of storage.

TABLE 9. Analysis of variance of treatment effects on fall 1989 height and root collar diameter (RCD) in western redcedar seedlings planted at the MB Harmac test site

Source	df	Fall height		Fall RCD	
		MS	F	MS	F
Bed	1	24462.51	34.83*	358.897	13.71ns
Replicate	2	467.90	0.67ns	6.177	0.24ns
Treatment	5	2372.39	12.54*	20.577	1.24ns
Storage	1	4014.68	2.16ns	243.726	3.89ns
B*R	2	702.40	0.66ns	26.174	2.01ns
B*T	5	547.81	0.52ns	12.604	0.97ns
R*T	10	698.65	0.66ns	17.100	1.32ns
B*S	1	2017.61	7.50ns	3.832	0.25ns
R*S	2	113.50	0.42ns	9.416	0.61ns
T*S	5	1804.61	2.36ns	62.590	2.33ns
B*R*T	10	1057.24	0.98ns	12.994	0.67ns
B*R*S	2	269.04	0.25ns	15.531	0.80ns
B*T*S	5	1334.00	1.24ns	37.103	1.92ns
R*T*S	10	509.27	0.47ns	9.115	0.47ns
B*R*T*S	10	1078.86		19.341	
	71				

* significant effect at $\alpha = 0.05$; ns = non-significant.

TABLE 10. End of first farm-field season, pooled mean total height and root collar diameter (RCD) by nursery treatment for western redcedar planted at Harmac test site

	Nursery Treatment[a]					
Morphological variable	1 Control	2 SD/ND Jun	3 AD/DR Jun	5 SD/ND Jul	6 AD/DR Jul	7 SD/DR Jul
Height	36.7a[b]	33.3b	35.8a	36.6a	36.3a	34.2ab
RCD	4.66a	4.34a	4.65a	4.70a	4.59a	4.55a

[a] See Table 1 for legend

[b] Means not followed by the same letter, significantly different using protected LSD at $\alpha = 0.05$.

TABLE 11. Analysis of variance of treatment effects on 1989 height, root collar diameter (RCD), and volume increments in western redcedar seedlings planted at the MB Harmac test site

Source		Height		RCD		Volume	
	df	MS	F	MS	F	MS	F
Bed	1	21305.30	42.93*	155.291	10.20ns	4888054	12.77ns
Replicate	2	497.36	1.00ns	14.403	0.95ns	269021	0.70ns
Treatment	5	543.18	0.73ns	10.152	0.45ns	339877	1.50ns
Storage	1	2807.75	27.20*	127.520	7.72*	3232975	10.74*
B*R	2	495.30	0.36ns	15.231	1.45ns	382736	0.43ns
B*T	5	859.04	1.36ns	17.235	1.65ns	278186	1.01ns
R*T	10	520.82	0.83ns	15.621	1.49ns	223553	0.81ns
B*S	1	67.24	1.07ns	12.751	0.67ns	61216	0.30ns
R*S	2	98.55	1.58ns	22.849	1.20ns	37545	0.19ns
T*S	5	1392.24	2.21ns	44.864	2.40ns	893110	7.00*
B*R*T	10	630.76	0.45ns	10.469	0.54ns	274598	0.59ns
B*R*S	2	62.56	0.04ns	19.084	0.99ns	202250	0.43ns
B*T*S	5	1023.90	0.73ns	29.731	1.53ns	491291	1.05ns
R*T*S	10	307.63	0.22ns	8.304	0.43ns	105268	0.22ns
B*R*T*S	10	1406.61		19.374		468987	
	71						

* significant effect at $\alpha = 0.05$; ns = non-significant.

TABLE 12. Pooled mean height and volume increments in response to storage and bed type after one growing season and the significance of the relationships

Morphological variable	Storage			Bed type		
	0 mos.	4 mos.	Sig.*	Dry	Wet	Sig.
Height (cm)	16.2	15.0	*	13.9	17.3	*
RCD (mm)	2.60	2.33	*	2.32	2.61	ns
Volume (cm^3)	2.09	1.67	*	1.62	2.14	ns

* significant effect at $\alpha = 0.05$; ns = non-significant.

4 DISCUSSION

4.1 Seedling Growth and Morphology

The usefulness of SD and DR to modify western redcedar seedling development is limited. The species growth habit is such that the treatments affect growth mainly within the time of treatment application.

Height is about the only character that can be effectively controlled by SD and DR. The combination of SD and DR has a synergistic effect; reducing height growth at almost any time, and allowing flexibility in time of application. The fact that early DR had little effect on the control of height is surprising. However, DR was critical in reducing height in SD + DR treatments. Height growth of open grown western redcedar has been correlated with current year temperature and rainfall (Williams 1968). Growth can be retarded by naturally occurring late summer moisture deficiency (Parker and Johnson 1987). Although SD alone can control height, its effect depends greatly on timing of application. It reduces height growth if applied during the time of the most rapid shoot growth in late June and early July. After that, SD results are ineffective and variable. It has been suggested (A. Mitchell, pers. comm., 1990) that the lack of SD effects at some times of the year may be related to the interactions between plant growth substances and nutrition. Difficulty in regulating seedling nutrition in western redcedar has been reported (J. Kumi, pers. comm., 1990).

Control of height growth was not improved with SD + DR treatments for 4 weeks. The relatively small differences in seedling morphology resulting from 4-week treatments compared to the differences from 2-week treatments, suggests that seedlings of western redcedar, after their initial reaction, are capable of considerable adaptation to the modified environmental conditions. Two-week treatments did not significantly alter seedling caliper and root dry weight. Four-week treatment durations were more deleterious to morphological characters, except height, than 2-week durations. For this reason, 4-week durations are not recommended for height control of western redcedar seedlings.

Reduction in height growth of western redcedar was caused more by reduced stem unit length than by fewer stem units. O'Reilly and Owens (1989) also noted that reduction in stem unit length contributed to the reduction in height growth of western hemlock seedlings exposed to different dormancy-inducing treatments. Treatment combinations that reduced height without reducing NSU apparently affected rates of cell enlargement rather than rates of cell division in shoot apex. However, precise evaluation of these processes is difficult in experiments where environmental conditions are only partially controlled. The environmental data indicated that the darkout greenhouse was generally warmer than the operational one. Perhaps this caused the observed increases in height growth during mid- and late summer SD applications.

Differences in numbers of initiated primary branches between treatments were small. In mature western redcedar, lateral branches are initiated in the axil of one leaf in every two to four pairs of leaves (Owens and Molder 1984). The same occurs in seedlings, where lateral branches are initiated in the axils of whorled and decussate leaves.

Late August DR hastened the rate of root dry weight growth. This could be an important factor, if seedlings are to be used for fall planting. Two-week application of SD, DR, and SD and DR together usually yielded seedlings with higher root dry weights than did 4-week applications. In western redcedar, reallocation of dry matter from stems to roots was not achieved to any degree by any 4-week treatments.

These observations agree with those of Grossnickle *et al.* (1988) for this species. Those authors noted that their observations contradicted the general belief that suppression of shoot growth shifts seedling growth potential to roots (Ledig *et al.* 1970; Tinus and McDonald 1979). Hawkins and Draper (1988), however, did find a shift in carbon allocation from shoots to roots in interior spruce seedlings after long blackouts. In response to SD treatments, species exhibiting preformed growth after the first year (e.g. spruce) may have different carbon allocation patterns compared to those species which do not form an embryonic shoot (e.g. cedar). Arnott *et al.* (1988) concluded that in western hemlock, SD affects phenology of growth, whereas moisture stress affects rates of growth. This may be true for bud-setting species, but not for species like western redcedar. Grossnickle *et al.* 1988 also did not observe changes in the phenology of shoot growth in SD- and DR-treated western redcedar. Treatments which influence the growth rate of western redcedar do so mainly during their application. The degree of influence depends on the time of treatment application.

If better quality western redcedar seedlings are required, then means other than SD and DR must be found. Plant growth regulators may be effective, but like SD and DR they may only be applicable as auxiliary treatments to alter seedling morphology. Their effects may depend on precision and timing of application.

Using larger cavities for seedlings of western redcedar may be one way of improving seedling quality. Larger root mass and caliper were formed in larger cavities for seedlings of Douglas-fir (van den Driessche 1982) and western hemlock (O'Reilly and Owens 1989). This approach has also been adopted by some nurseries for western redcedar (T. Hale, pers. comm., 1987). Increased seedling height may be an undesirable side effect of increased cavity size. However, SD + DR for 2 weeks during most rapid height growth, followed towards the end of the growing season by a 2 week period of mild drought, may reduce the height and produce seedlings with good morphological characteristics.

4.2 Mitotic Activity, Root Growth Potential and Dormancy Status

Mitotic activity in western redcedar terminal apices is cyclic during the growing season. The highest MI occurred during the most rapid shoot growth in early summer; reduced MI occurred roughly during more intense periods of root growth during summer. The treatments did not have a lasting effect on MI of terminal shoot apices.

The observed differences at the time of treatments are difficult to evaluate, especially through weekly sampling done only at one time of the day. It is possible that altered day length shifted the daily course of MI, so it is not known whether the observed rates in treated and untreated seedlings are comparable. For such an evaluation, a laborious study would have to be undertaken to determine diurnal patterns of MI under different photoperiods. For this reason, the usefulness of MI trials based on weekly or even daily collections for evaluation of growth rates is questionable if various cultural regimes are to be compared.

Changes in apical dimensions followed the same pattern as changes in MI. Terminal apices were the largest in the spring and summer when MI was high and the smallest in late fall and early winter when it was low. Owens and Molder (1973) observed similar changes in apical dimensions in apices from mature Douglas-fir. In species that have preformed embryonic shoots, such as Sitka spruce, size of the apical dome is believed to be related to the rate of initiation and size of initiated primordia (Cannell 1978). In western redcedar there is little chance of the apex being "used up" by initiated leaf primordia since the apical dome is constantly renewed after initiation of each whorl or pair of leaves. The observed decrease in apical dimensions in the fall in western redcedar reflects the lower rates of apical enlargement resulting from lower MI.

The MI was a better way to estimate the dormancy status than was a measurable shoot elongation. In our dormancy release trials, mitotic activity always preceded measurable shoot elongation by a few days. The lack of mitotic activity was always accompanied by the lack of visible growth. Since placing western redcedar seedlings under favourable growth conditions always resulted in growth resumption, we have concluded that the seedlings were not truly dormant in the sense of dormancy definitions presented by Molish (1922) and Doorenbos (1953). However, there is apparently some endogenous control involved in maintaining an inactive growth status of western redcedar seedlings in winter, not just a lack of appropriate growing conditions. This is evident in the December dormancy release trial where resumption of shoot elongation by the leader at 20°C under the 8-h photoperiods was much more delayed than in seedlings under the 16-h photoperiod. In January and February trials, however, the time until the terminal shoot apex resumed growing was shorter than in December. In February, the difference in the height achieved was likely due to a longer photoperiod at 16-h than at 8-h.

The results obtained in our study are similar to those of Garber (1983). In his study, a longer photoperiod partially substituted for the chilling requirement needed for growth by container-grown loblolly pine (*Pinus taeda* L.) seedlings, but the photoperiod did not affect the time until growth resumed once the chilling requirement was satisfied. Lavender and Hermann (1970) reported similar findings in Douglas-fir. Perhaps terminal apices of western redcedar have an early winter chilling requirement and long photoperiods can substitute for this requirement. Only terminal apices are concerned, however, since growth resumed in laterals rapidly under both photoperiods and at all times during winter. The more prompt growth response in lateral buds compared to that in the terminal buds has also been reported for some species of Pinaceae such as coastal Douglas-

fir (Lavender and Hermann 1970) and *Abies* (Tung and DeYoe 1988). This suggests that factors inhibiting growth resumption in winter are localized more in terminals than in laterals. It is not clear, however, whether the laterals have no chilling requirement or just less chilling requirement than terminals. Perhaps a "neutral" rather than extended photoperiod should be recommended for dormancy release trials.

The seedlings were not kept at the typical cold storage conditions, but rather at conditions similar to those of non-lifted seedlings remaining in styroblocks under fairly low winter temperatures. Root growth potential of these seedlings was very good in the December and February trials and differences due to photoperiod were smaller than those observed in shoot growth responses. In January, roots kept at an 8-h photoperiod had lower growth potential than in December and February. This possibly indicates the existence of endogenous mechanisms which could prevent growth resumption during unusually high winter temperatures. The control of shoot and root growth in response to favourable growth conditions in winter is different. Further investigation is needed to explain the value of root growth potential (RGP), which has recently been subjected to criticism (Landis and Skakel 1988; Binder *et al.* 1988).

The results of our study also indicate the need to standardize conditions for such trials. Grossnickle *et al.* (1988) noted that conditions, particularly temperature, used in RGP trials are often not related to the real conditions which seedlings would be subjected to at outplanting. The possible endogenous regulation of root response to RGP conditions may be one cause of the confusion experienced in such trials and therefore RGP tests should not be the only criterion in the evaluation of seedling quality.

4.3 Leaves

Leaves of western redcedar have been described in a number of studies (Laubenfels 1953; Franklin 1961; Owens and Pharis 1971; Parker and Johnson 1987). The first true leaves exhibit typical features of juvenile leaves, except they are initiated as a pair. Parker and Johnson (1987) noted that juvenile leaves usually occurred in whorls of four, although individuals with whorls of three were also found. In this study, whorls of four leaves occurred most commonly during early seedling development and later whorls of three were initiated. This suggests the number and sequence of whorled-leaf initiation in western redcedar may display phenotypic plasticity.

The apical transition between the initiation of juvenile and the initiation of mature leaves does not always occur during the first growing season. Less vigorous seedlings produced mature leaves only on laterals during the first year, whereas more vigorous seedlings underwent transition from juvenile to mature foliage in the first year. This transition was delayed by a short photoperiod and drought applied in early summer. Any differences in photosynthetic and transpiration capacities between juvenile and mature leaves could be of importance to the nursery grower and field forester.

Stomata were present on both leaf surfaces in juvenile and mature leaves and were more abundant on the abaxial surface. Cotyledons, in contrast, had stomata only on the adaxial surface. This is not surprising since, in contrast to the true leaves, the abaxial surfaces of cotyledons are exposed during germination, therefore, the lack of stomata on the abaxial surface protects germinants from excessive transpiration during this sensitive period of development.

4.4 Epicuticular Waxes

Studies of leaf surfaces are used for taxonomic purposes (e.g., Stockey and Ko 1988). Properties of epicuticular waxes are also related to light reflectance (Reicosky and Hannover 1978), transpiration and gaseous exchange (Baker 1974), and infections by pathogens (Martin and Juniper 1970). Only surface features of epicuticular waxes and the incidence of plugged stomata under stress and non-stress conditions were compared in our study.

In a similar study of western hemlock seedlings, O'Reilly *et al.* (1989) found little difference in wax configurations and cuticle thickness between leaves from SD and DR nursery-treated seedlings. Therefore, no attempt was made in our study to measure thicknesses of cuticle and wax layers or to examine wax chemistry. In western redcedar, more frequent and massive coalescence of wax into crusty configurations was found on leaves initiated during and after drought stress than on leaves of untreated seedlings. This

suggests that greater secretion of waxes may be triggered by drought. The incidence of plugged stomata was extremely low on both leaf surfaces of juvenile and mature leaves regardless of the treatment. Formation of wax plugs does not occur in all species (Stockey and Ko 1988), however Martin and Juniper (1970) showed that characteristics of epicuticular waxes may differ between greenhouse and natural environments. Indeed, high pressure watering and application of pesticides and nutrients with nursery watering may have a significant effect on wax features. The crumbled wax layer observed on the adaxial leaf surfaces in western redcedar may be related to those factors.

4.5 Frost Hardiness and Field Performance

Stock treated with drought in the nursery was slow in acquiring foliage frost hardiness at the time of lifting, compared to stock undergoing other nursery treatments (Table 9). Presumably this occurs because drought treatments temporarily reduce productivity and frost hardiness induction in an energy-requiring process (Blake *et al.* 1979). This suggests the drought treatment resulted in less dormant nursery stock, if one accepts the hypothesis that dormancy and frost hardiness induction are coincidental processes (Fuchigami and Nee 1987). Seasonal mitotic indices in 1987 did not distinguish any treatment-induced differences in the level of meristematic activity (Figure 18). The same was true at lifting in 1988. Perhaps in an indeterminate species, such as cedar, dormancy and frost hardiness induction are affected differently by nursery-applied moisture stresses.

Frost tolerance increased during storage for seedlings from the two drought treatments, but decreased in stock from the other nursery treatments (Table 9). If the different pattern is related to chilling sums (Ritchie 1989), then drought-treated seedlings did not acquire their chilling units as quickly as other stock when exposed to the same post-treatment environment. This again raises the question: Are different levels of frost hardiness indicative of different dormancy levels, even though there was no difference in mitotic activity? The answer should become apparent after 4 months of cold storage at +2°C, since dormancy intensity and storability are well correlated (Ritchie *et al.* 1985; Ritchie 1989). As there were no survival differences between nursery treatments after one field season, one must assume that the alteration to frost hardiness induction had no effect on seedling storability, and hence on level of dormancy (Ritchie *et al.* 1985; Ritchie 1989).

End of first field season height by nursery treatment, while statistically significant (Table 10), is likely of no practical importance because the mean treatment range was less than 4 cm (Table 11). Generally, the tall and short stock from the nursery was still the tallest and shortest after one farm-field season (Figure 7; Table 11). A similar generality can be made about RCD. In terms of storability, if height and RCD are used as gauges, it is clear that all nursery treatments had enough stress resistance to be stored for at least 4 months, a very long storage duration for western redcedar. Perhaps all stock was lifted before it achieved its maximum level of dormancy intensity, and therefore it stored well (Fuchigami and Nee 1987; Ritchie 1989).

In the short term, it is the growth increment rather than absolute height or diameter, that the forester should be concerned about. Non-stored stock had significantly greater height and RCD increments than did stored stock (Table 12), but measurable differences were likely of no practical significance (Table 13). This is in agreement with earlier work on western redcedar (Hawkins 1989) which indicated that 5 weeks of storage marginally enhanced first field season performance. Cedar can therefore be safely stored for up to 4 months without first-year performance being affected, provided it is lifted with high levels of stress resistance and handled carefully.

Stock planted in the wet bed had a statistically greater height increment (Table 13) than that planted in the dry bed, but again this is of little practical importance. A similar result was observed for the 1987 nursery treatments planted in 1987/88 (Hawkins 1989). It is not surprising that stock planted on a low stress site outperforms the same stock planted on a site with a higher level of stress.

The nursery treatments, while statistically significant, had little or no practical impact on 1989 farm-field performance. This is partly a reflection of:

- the growing season, where no extended periods of high light were observed to maximize dry bed stresses; and,

- the time of measurement, where assessments were done in September to meet FRDA requirements and active growth continued until at least early December in 1989.

These trees will be remeasured in late November 1990 after another year under wet and dry bed conditions. Only then will the importance of the nursery treatments be ascertainable.

5 CONCLUSION

Shoot development in the Cupressaceae is adapted to an opportunistic form of growth. There is no fixed growth periodicity and no variation in foliar organs (bud scales and preformed leaves). Shoots, like roots, are capable of rapid response to short-term environmental changes. In western redcedar, unlike in determinate species, these changes do not fix the shoot in any irreversible morphogenetic growth pattern. As this study shows, dormancy induction methods effective for species having preformed bud growth cannot be readily adapted for dormancy induction in species with an indeterminate, opportunistic growth habit. End of season applications of SD and/or DR might be more effective in dormancy induction in these species. The use of SD and DR during mid-growing season is limited to the control of height growth.

Nursery treatment had no practical impact on subsequent farm-field performance under the test conditions. Western redcedar, when lifted at the correct stage of dormancy and stress resistance, can be safely stored up to 4 months without affecting first-year growth.

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